Great Basin Naturalist 53(1), pp. 59–72

CYANOBACTERIA AND CYANOLICHENS: CAN THEY ENHANCE AVAILABILITY OF ESSENTIAL MINERALS FOR HIGHER PLANTS?

Kimball T. Harper[1] and Rosemary L. Pendleton[2]

ABSTRACT—In both field and greenhouse studies, cyanobacteria and cyanolichens of cold-temperate deserts often enhance growth and essential element uptake by associated herbs. That effect is associated with better seedling establishment and larger seedlings. The following are possible mechanisms for these effects: (1) the microbiota concentrate essential elements in available forms in soil surface layers, (2) the microbial surface covers are usually darker colored than the soil itself and produce warmer soils during cool seasons when soil water is most available, (3) the gelatinous sheaths of several cyanobacterial genera common on alkaline deserts contain chelating compounds, and (4) conditions that favor persistent microbial growths on soil surfaces also favor maintenance of larger populations of microorganisms that form mycorrhizal and/or rhizosheath associations with seed plants. There is evidence that associated animals may be nutritionally benefited by the enhanced mineral content of forage plants growing in well-developed cyanobacterial crusts.

Key words: cryptogamic crusts, mineral uptake, plant nutrition, plant growth, mycorrhizae, deserts, cyanobacteria, Collema, Microcoleus.

Dense growths of cyanobacteria, lichens, xerophytic algae, mosses, and microfungi are a common feature of soil surfaces in semiarid and arid temperate regions worldwide (Friedmann and Galun 1974, Harper and Marble 1988, West 1990). Such soil covers are commonly much darker than associated surfaces without such growths (Fig. 1). Previous work on these cryptobiotic surface growths (or "cryptogamic crusts" as they are often called) has focused on their ability to "fix" nitrogen in a biologically available form (MacGregor and Johnson 1971, Mayland et al. 1966, Shields and Durrell 1964) and to stabilize soil surfaces against water (Booth 1941, Fletcher and Martin 1948, Fritsch 1922) or wind erosion (MacKenzie and Pearson 1979). Other studies have shown that nitrogen fixed by cyanobacterial components of the cryptobiotic crusts is available to higher plants (Fuller et al. 1960, Mayland and MacIntosh 1966, Stewart 1967).

The intent of this paper is to assemble existing data and report new data bearing on the influence of cyanobacterial-rich assemblages of cryptobiota on mineral nutrition of associated vascular plants.

PERTINENT LITERATURE

A large literature documents the role of cyanobacteria, cyanolichens, and free-living bacteria (nonsymbiotic) in desert soils (Harper and Marble 1988, West 1990). Since legumes and other vascular plants that form symbiotic, nitrogen-fixing associations with bacteria are uncommon in cold-temperate deserts, their importance as sources of biologically available nitrogen is minimal in such environments (West 1981). Rychert et al. (1978) concluded that "blue-green algae"–lichen crusts fix significant amounts of atmospheric nitrogen in desert soils (they estimate fixation of 10–100 kg N $ha^{-1} yr^{-1}$ in the Great Basin of North America). Available information suggests that nonsymbiotic, heterotrophic nitrogen fixers are responsible for fixation of only ≤2 kg N $ha^{-1} yr^{-1}$ in North American deserts (Rychert et al. 1978, Steyn and Delwiche 1970). The input of available nitrogen in annual precipitation is apparently low, with estimates running from 4–6 kg $ha^{-1} yr^{-1}$ (West 1978) to 1–2 kg $ha^{-1} yr^{-1}$ (Schlesinger 1991). Schlesinger (1991) notes that available N in dry-fall exceeds that in rainfall in some areas, but West and Skujins (1978) argue that since deserts produce

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602

[2] Shrub Sciences Laboratory, Intermountain Research Station, USDA Forest Service, 735 North 500 East, Provo, Utah 84606

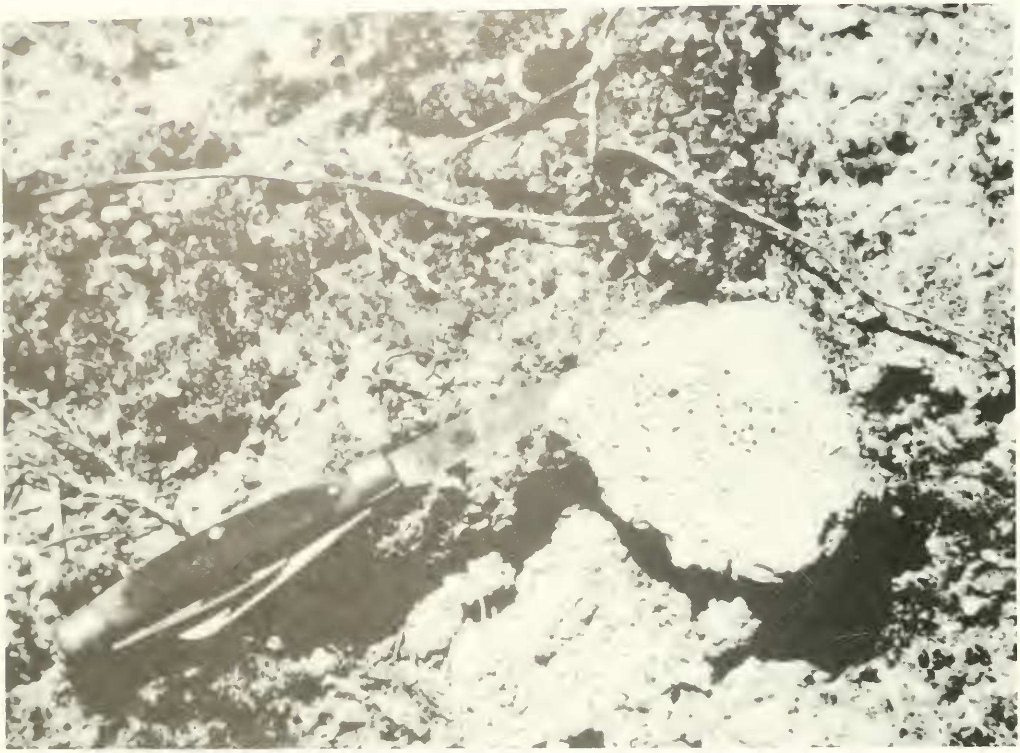

Fig. 1. Contrast between natural soil color and the dark-colored cryptobiotic growth on the soil surface. Such surface growths of cyanobacteria, the black lichen *Collema*, and xerophytic mosses are common on desert soils in the Intermountain West of North America. Soil shown is developed from ancient lacustrine deposits, western Utah.

more dust than they receive, N in dust (the primary source of N in dry-fall) probably represents a net export from deserts. Denitrification processes are active in deserts and may equal or exceed rates of fixation (Skujins and Klubek 1978).

It is estimated that vascular plants take up 10–12 kg N ha⁻¹ yr⁻¹ in the cold deserts of the Great Basin (West and Skujins 1977). We can infer from work by Romney et al. (1978) that annual uptake of N by vascular plants in the warm deserts of the northern Mohave is slightly greater than that reported by West and Skujins (1977) for cold deserts. In either case, annual uptake is greater than the combined total of new nitrogen added by precipitation and heterotrophic bacteria. Since the amount of N fixed by symbiotic organisms is apparently trivial in desert [illegible] Great Basin and the northern Mohave [illegible] cyanobacteria-lichen [illegible] deserts (Rychert et [illegible]

The ability [illegible] [illegible] San

surface soils of deserts has been documented in a variety of reports. Such studies often show that available P, exchangeable K, and surface soil organic matter increase apace with cryptobiotic cover (Anderson et al. 1982, Kleiner and Harper 1972, 1977a, 1977b, McKnight 1980). The trend for elements other than N is apparently related, at least in part, to the tendency of the cryptobiotic crusts to trap soil fines (silt and clay) and to sequester essential elements in living cells (Fletcher and Martin 1948, Kleiner and Harper 1972).

Cryptobiotic crusts are usually darker than associated soils in deserts (Fig. 1). As a result, soil surfaces covered by such crusts absorb radiant energy better than nearby uncrusted soils and are warmer (Kleiner and Harper 1977b, Harper and Marble 1988). Temperature differences may be at least 5°C (Harper and Marble 1988) and are probably greatest in cooler seasons. In the Great Basin, where the bulk of biologically usable moisture accumulates from winter storms, areas covered by cyanobacterial-*Collema* lichen crusts can be expected to be significantly warmer than interspersed uncrusted soils. Both soil microbes and associated vascular plants (especially shallowly rooted species and seedlings) should experience accelerated spring growth on sites where soil temperature is elevated because of well-developed cryptobiotic growth. Enhanced growth of seed plants rooted in cryptobiotic crusts might be expected because of more favorable temperatures and more fertile soils. Physiologists have long recognized that many physiological processes have a Q_{10} of 2–3; that is, as temperatures within the range of easy tolerance are increased 10°C, metabolic rates for processes such as enzymatic reactions, ion uptake, and ion transport are doubled or tripled (Glass 1989).

Algologists and microbiologists have documented the nature of organic secretions from microorganisms and speculated on their ecological roles in the organism-environmental complex. Algae are known to secrete polysaccharides, amino acids, vitamins, growth factors, steroids, saturated and unsaturated fats, and other beneficial or toxic compounds of unknown structure (Lefevre 1964). The secretions often form a gelatinous film around the cells. Among cyanobacteria, such sheaths are common and include polysaccharides, organic acids, amino acids, and polypeptides (Lange 1974). In aquatic systems, extracellular organic secretions play a variety of roles including food for heterotrophic organisms, chelating agents that increase availability of essential elements (particularly iron and other trace elements), growth stimulators, toxic compounds that discourage herbivory (and are sometimes autotoxic), and compounds that complex with and inactivate toxic agents (such as copper) in water (Lefevre 1964).

Lange (1974) demonstrated that sheath materials of cyanobacteria include chelating agents that permit the organisms to grow vigorously in water having a high pH in which several essential elements would otherwise be available in such low amounts that active growth would be impossible. He demonstrated that some species in each of the following genera secreted enough natural chelators to produce growth equivalent to that of the same species in cultures that received artificial chelators: *Anabaena*, *Anacystis*, *Lyngbya*, *Microcystis*, and *Nostoc*. He also demonstrated that the natural chelators were water soluble and that filtrates of cultures in which chelating species had grown supported good growth of nonchelating species. The latter species were unable to grow in the same water if chelating species had not previously grown in it. Lange (1976) concluded that the gelatinous sheaths of cyanobacteria provide a microenvironment around their cells, where essential nutrients can be concentrated from an environment in which those elements exist at levels too low to sustain growth. In alkaline deserts the hygroscopic nature of the copious gelatinous sheaths produced by cyanobacteria (and many associated algae, bacteria, and fungi) suggest another, perhaps essential, role for such extracellular secretions, that of retaining enough water around cells in dry periods to prevent lethal desiccation.

A large literature documents the important role of mycorrhizal associations for mineral nutritional relationships of vascular plants (Allen 1991). Allen (1991) concluded that "major perturbations almost always reduce the inoculum density" of mycorrhizal fungi. Bethlenfalvay et al. (1985) determined that trampling of soils by hoofed grazers (cattle) reduced mycorrhizal inoculum in crested wheatgrass pastures in Nevada. Koide and Mooney (1987) showed that pocket gopher burrowing in otherwise undisturbed serpentine herblands in coastal California also reduced mycorrhizal inoculum. Perry et al. (1989) reported that sprouting shrubs may maintain a mycorrhizal infection through the stressful conditions induced by wildfire. Wullstein and Pratt (1981) discussed the development of rhizosheaths of *Oryzopsis hymenoides* (R. & S.) Riker (now classified as *Stipa hymenoides* R. & S.), a desert grass. *Oryzopsis* and several other grasses of arid, sandy soils produce conspicuous rhizosheaths consisting of dense tangles of root hairs and intermixed heterotrophic bacteria capable of fixing nitrogen (Wullstein et al. 1979). Unpublished data in the files of the senior author suggest that rhizosheaths apparently enhance mineral uptake of *Stipa hymenoides* for several elements.

The foregoing literature survey suggests that cryptobiotic crusts may significantly alter the uptake of essential elements by associated desert seed plants. In this paper we report preliminary results on the effects of cryptobiotic covers dominated by cyanobacteria and *Collema* on tissue chemistry of associated seed plants. *Collema* is a black-colored lichen in which the photobiont is the cyanobacterium *Nostoc*. Specifically, we will consider the effects of the

TABLE 1. [illegible] *Collema* cover [illegible] surface layer of sand. [illegible] for comparison [illegible] free of surface growth by [illegible]. The values for each surface condition are averages of 14 samples collected at three [illegible] southeastern Utah. Two composite samples were taken on each surface condition at Wind Whistle Campground, San Juan County, and 12 composite samples were taken from blow sand and nearby soils stabilized by cryptobiotic cover at two locations in Arches National Park, Grand County, Utah.

Characteristic	Blow sand	Cyanobacterial-*Collema* sand
Sand (%)	92.7	79.1
Reaction (pH)	7.8	7.2
	Percent (%)	
Organic matter	0.57	0.93
Nitrogen	0.008	0.021
	PPM "available"	
Calcium	1,449	3,784
Copper	0.20	0.21
Iron	8.1	7.5
Magnesium	39.0	57.0
Manganese	1.6	15.4
Phosphorus	23.7	51.8
Potassium	69.7	87.0
Sodium	8	10
Zinc	0.5	0.3

cryptobiotic cover on soil fertility, soil temperature in the cool season, possible chelation effects, and colonization of seed plant roots by microorganisms.

METHODS

Soil samples considered in Tables 1 and 3 consisted of composite samples of the surface 5 cm of the profile taken at 10–12 randomly chosen sites within each of the following surface conditions: areas that supported a well-developed (i.e., >90%) cover of cyanobacteria and the lichen *Collema tenax*, and areas only [illegible] where prevailing winds or [illegible] development. All soil samples [illegible] were collected in [illegible] identified in the legend of Table 1.

[illegible] determined using a hydrometer [illegible] taken with [illegible] paste. Organic matter was estimated by digestion with 1.0 N potassium dichromate. Total soil nitrogen was analyzed by the micro-Kjeldahl procedure. Phosphorus was determined with the iron-TCA-molybdate method on a soil extract taken with 0.2 N acetic acid. Exchangeable bases were freed from the soil with 1.0 N ammonium chloride. Ion concentrations in the extract were estimated by atomic absorption. All soil analyses were made in the Soil and Plant Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University, and all analytical methods were based on those recommended by Black et al. (1965).

Soils for pot trials in the glasshouse were bulk-collected from the Sand Flats site, Grand County, Utah, in January 1991 and immediately spread in a thin layer on a laboratory floor to air-dry. Samples from areas with and without cryptobiotic cover consisted of the surface 5 cm only. Once dried, soils from each surface type were thoroughly mixed (including the biotic cover for that sample set) to ensure a uniform potting mixture. No fertilizer amendments were added. Subsamples from each surface type were taken for subsequent analysis of physical and chemical characteristics. One liter of soil from the sample taken from each surface type was placed in a drained plastic pot having a top diameter of 15 cm. Before pots were filled, drainage holes were covered with a coarse fiberglass mesh to preclude loss of soil. Soils from each surface type were replicated 10 times in individual pots. Pots were immediately placed in a grid on a water-tight table in a glasshouse and watered from the bottom with a 2.5-cm layer of water that was drained off as soon as soil at the pot surface was thoroughly wetted by capillarity. Pots were placed in a 4 × 5 grid with grid intersections 30 cm apart. Cryptobiotic and blow sand soil surface types were alternated in the grid. Six presoaked seeds of *Sorghum halepense* (L.) Pers. were planted in each pot on 11 February 1991. Pots were irrigated with tap water as needed to maintain nonstressful growing conditions.

To evaluate the effects of cyanobacterial growth throughout the rooting zone, we initiated a second trial simultaneously with the foregoing pot trials. In that trial we filled narrow, glass-walled planters with 0.9 liter of the same cryptobiotic-covered soil. Each planter was 1.5 cm wide, 40 cm long, and 30.5 cm deep and was divided into two compartments of equal size by a redwood strip 1.5 × 0.5 × 30.5 cm inserted at the midpoint of the planter before adding soil. The glass walls of one compartment of each planter were covered with aluminum foil to exclude light. Planters were drained and aerated at their bottoms via a perforated tygon tube (4 mm in diameter) open to outside air at both ends. These planters were irrigated and planted with presoaked *Sorghum halepense* seed at a rate of 6 seeds per compartment on 16 February 1991. This trial was replicated 10 times. It was necessary to water these planters on alternate days with 250–300 ml of water. For convenience, tap water was drawn and stored in a plastic bucket in the glasshouse until needed for irrigation of planters. This water averaged 8–12°C warmer than water taken directly from the tap. The combination of warmer irrigation water and less exposed soil surface from which water could evaporate resulted in root temperatures for plants grown in narrow planters that averaged 3–8.5°C warmer than those of *Sorghum* plants from the same seed lot grown in the same soil but watered from the bottom. Temperature differences were greatest immediately after irrigation of the pots with cold tap water.

After three weeks cyanobacterial growth covered the glass walls of planters not covered by aluminum foil. The cyanobacteria obviously competed with *Sorghum* roots for essential minerals. Plants grown in planters that received light throughout the rooting zone were smaller, and their leaves were discolored by reddish pigments in contrast to adjacent plants grown under identical conditions except that light was excluded from the rooting zone. As a consequence, glass walls of all planter compartments were covered with aluminum foil 3 weeks after planting. The foil remained in place until plant top growth was harvested for analysis on 29 April 1991. Plants grown in planter compartments previously illuminated in the rooting zone quickly regained normal leaf color and became indistinguishable in size from adjacent plants grown in compartments with foil-covered rooting zones. Chemical analyses of plant tissue from these trials demonstrated that tissue chemistry from plants that had their rooting zone exposed to light for 3 weeks did not differ significantly for any element considered from that of plants that had not received light at any time in the rooting zone.

Plants in narrow planters and those in pots of bottom-irrigated, cyanobacterial-enriched soil were grown from the same seed lot in the same soil and were propagated in the same glasshouse at the same time. These otherwise identical conditions for growth were marked by a strong difference in root temperature, with pots averaging ~16°C and narrow planters ~21°C. To determine the effect of different rooting zone temperatures on mineral composition of *Sorghum* aboveground growth, we analyzed and compared the chemical composition of top growth of pot-grown plants and planter-grown plants (see Results).

Plant tissue was oven-dried at 60°C for 12 hr and then ground in a steel rotary mill using a 40-mesh sieve. Samples were stored until analyzed in capped plastic vials. Tissue nitrogen was determined using micro-Kjeldahl procedures. Duplicate 1.0-g tissue samples from each experimental replication were digested in a 1:5 solution of concentrated sulfuric and nitric acid. Content of bioessential elements in the digestate was determined using atomic absorption procedures (Page et al. 1982).

The degree of root infection by vesicular arbuscular mycorrhizae and other root symbionts such as *Rhizobium* bacteria (associated with roots of *Lupinus*) or *Bacillus* bacteria (associated with rhizosheaths of *Stipa hymenoides*) was determined by microscopic examination of roots of randomly selected plants growing in well-developed cyanobacterial-*Collema* crust or on nearby comparable sites where wind action or animal traffic (sometimes areas trampled by people) had precluded growth of cryptobiota. Within each soil surface type, plants were randomly selected using the quarter method (Cottam and Curtis 1956). Plants were collected during early flowering (early May 1992) in Washington and Grand counties, Utah. *Bromus tectorum* L., *Cryptantha pterocarya* (Torr.) Greene, *Cryptantha crassisepala* (T. & G.) Greene, *Festuca octoflora* Walter, *Lupinus pusillus* Pursh, and *Plantago patagonica* Jacq. were collected in Washington County. *Coleogyne ramosissima* Torr., *Mentzelia albicaulis* Doug. ex Hook., *Stipa hymenoides*, and *Streptanthella longirostris* (Wats.) Rydb. were collected in Grand County.

Using a shovel, we lifted the root systems from the sandy soils in a block and then freed them from associated sand by hand. Plant tops were immediately excised and roots were placed in 75% ethanol in labeled, screw-cap glass

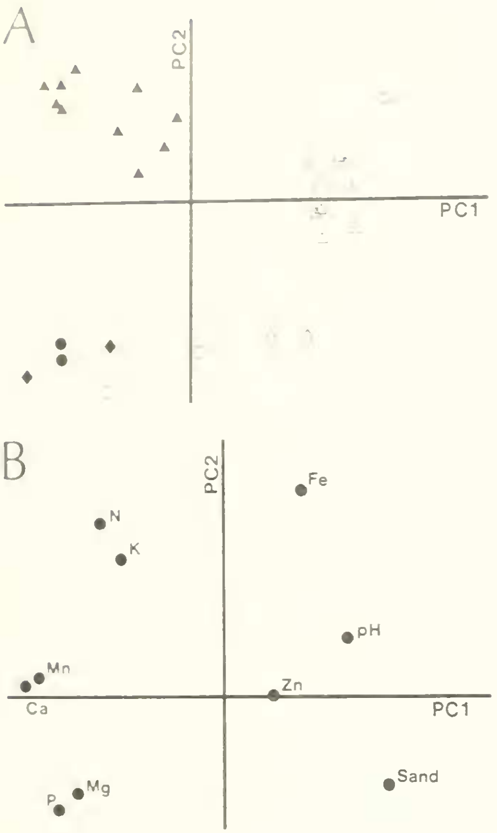

Fig. 2. A, plot of the first two components of soil samples from cryptobiotically crusted and uncrusted surfaces (for additional locations see Table 1). Samples from Arches National Park are indicated by triangles and diamonds; samples from Wind Whistle Campground are represented by circles. B, plot of weights of individual parameters used to construct the first two components shown in Figure 2A (see text for explanation).

sample jars. All soil samples were taken from the surface 1 cm of soil.

In the laboratory, samples were cleared and stained prior to microscopic evaluation of the amount of [illegible] on roots. Clearing and staining were accomplished using techniques described by Kormanik [illegible] 1980. Using the modified grid intersect method of Ambler and Young (1977) [illegible] and Mosse [illegible] [illegible] percentage of root length [illegible]. The [illegible] [illegible].

Plant nomenclature follows Welsh et al. (1987). Lichen nomenclature follows Egan (1987). Statistical significance of differences between group means was determined using an unpaired *t*-test model (Snedecor and Cochran 1967). Significance of treatment effects in Table 5 was determined using analysis of variance (ANOVA) with species treated as blocks. Percentage data were arcsine transformed prior to analysis by the GLM procedure of the SAS statistical package.

Centered, standardized principal components analysis (PCA) was used to analyze differences among samples collected from crusted soils and uncrusted soils (Pielou 1984). Various soil chemical and physical parameters were used in this analysis, which was conducted using the Statgraphics package.

RESULTS

The effect of cryptobiotic growth on surface soil chemistry and texture is particularly impressive for such variables as organic matter, soil N, exchangeable Mn, and "available" P (Table 1). Exchangeable Ca was also much higher on average in soils stabilized by cyanobacterial-rich surface growth. As in other studies (Fletcher and Martin 1948, Kleiner and Harper 1972, 1977a, 1977b), our results show that soil silt and clay are much greater in soils stabilized by cryptobiotic growth. The response of Ca, Mn, and P may be related to textural differences alone (Black 1968), but the increase in soil organic matter and N is probably directly related to the presence of cryptobiota.

Principal components analysis of the basic data on which Table 1 is based showed marked differences between crusted and uncrusted soils, even though three separate areas (two in Arches National Park and one at Wind Whistle Campground) were studied. The first principal component clearly separated the crusted soils of the most intensively sampled Arches site from the corresponding uncrusted soils samples (Fig. 2A). Crusted and uncrusted soils of the other two sites were also separated by the first component. Clear differences among sites were evident in the separation that occurred on the second principal component (Fig. 2A). The percentages of variance in the data accounted for by PC1 and PC2 were 48% and 22%, respectively.

TABLE 2. Tissue elemental content of plants of *Festuca octoflora* (a diminutive annual) and *Mentzelia multiflora* (a short-lived perennial herb) grown on blow sand and nearby sand stabilized by cyanobacterial-*Collema* crusts. The *Festuca* samples were taken at Wind Whistle Campground in San Juan County, Utah; the *Mentzelia* samples were taken at Courthouse Wash Dunes, Grand County, Utah. All data are from Belnap and Harper (in review). All tissue concentrations are expressed as amount per unit dry weight of aboveground growth and attached root tissue brushed free of sand. Sample size was 5 for each mean.

	Festuca octoflora			***Mentzelia multiflora***		
	Soil surface condition			Soil surface condition		
Element	Cyanobacteria/ lichen cover	Blow sand	Sign. differ.	Cyanobacterial/ lichen cover	Blow sand	Sign. differ.
N (%)	2.25	1.95	°	2.61	2.18	°°
P (%)	0.25	0.14	°°°	0.20	0.24	°°
K (%)	1.88	1.64	°	3.04	2.67	NS[a]
Ca (%)	0.65	0.52	°°°	2.50	1.97	NS
Mg (%)	0.15	0.13	°°	0.33	0.23	°
Cu (ppm)	11.0	10.4	NS	8.6	9.0	NS
Fe (ppm)	300.3	149.4	°	639.8	465.4	°
Mn (ppm)	60.3	74.0	NS	98.2	82.4	NS
Na (ppm)	61.5	59.8	NS	77.2	63.4	°
Zn (ppm)	43.0	33.0	NS	22.0	20.0	NS

°Means significantly different at $p < .05$

°°Means significantly different at $p < .01$

°°°Means significantly different at $p < .001$.

[a]Means not significantly different

Plotting the component weights (Fig. 2B) yields an explanation for the separation of crusted and uncrusted soils. The first component most clearly represents the differences between uncrusted and crusted soils. Uncrusted soils have higher values on this axis, which means they have higher pH and sand content (positive weights) and lower Ca, Mn, P, Mg, N, and K (negative weights). Iron and Zn tended to be higher in uncrusted soils but were not as important in separating points on the first axis. The second component most clearly represents site-specific differences. One Arches site (triangles in Fig. 2A) had higher N, K, and Fe (positively weighted) and lower P, Mg, and sand (negatively weighted) than the other two sites (Fig. 2B). The principal components analysis shows that despite some site-specific differences, crusted soils are generally higher in some essential minerals (N, K, P, Ca, Mg, Mn) than are uncrusted soils. Site differences were also clearly delineated in the analyses.

Table 2 clearly shows that cryptobiotic crusts do have a significant influence on tissue content of several bioessential elements in both *Festuca octoflora* and *Mentzelia multiflora* (Nutt.) Gray. Since Belnap and Harper (in review) show that soil textural differences are small (<10% difference in percentage sand) between blow sand and adjacent sands stabilized by surface growth of cryptobiota, the tissue content differences seen in Table 2 would seem to be strongly influenced by microorganisms on the soil surface. Tissue content of both seed plants was significantly greater for N, Mg, and Fe when plants were rooted in cyanobacterial-rich crusts. Although not all differences were statistically significant, 9 of 10 elements were present in greater amounts in tissue of *Festuca* plants grown on cryptobiotically stabilized surfaces; 8 of 10 elements were present in greater amounts in tissue of *Mentzelia* plants grown on the cryptobiotic surfaces. Finally, the data suggest possible competition between cryptobiota and seed plants for P and Mn. We also note that the responses of *Festuca* and *Mentzelia* were unalike in respect to P and Mn uptake.

Glasshouse trials demonstrate the soil "fertilization" effect of the cyanobacterial-*Collema* cover for growth of *Sorghum* (Tables 3, 4). Differences observed between chemistry of cyanobacteria-free and cyanobacterial-*Collema*–covered soils (Table 3) are small. The cryptobiotic-covered soil had slightly more N, P, K, and Na. The soil free of cryptobiotic growth averaged somewhat higher in Ca and Fe than the samples supporting cryptobiotic growth.

TABLE 3. Characteristics of cyanobacterial-*Collema*-[illegible] soil [illegible] cryptogamic soil [illegible] same depth [illegible] not colonized by cryptogams. [illegible] Samples are from Sand [illegible] County, Utah. Values for cations are amounts exchangeable in 1.0 N NH_4Cl. These are the soils on which *Sorghum bicolor* tissue considered in Table 4 was grown.

	Surface condition	
Soil characteristic	Free of cryptobiotic growth	Heavy cyanobacterial-*Collema* cover
Texture (% sand)	58	61
Reaction (pH)	7.5	7.4
Organic matter (%)	1.00	0.95
N (%)	0.038	0.043
Ca (ppm)	2,670	1,845
Cu (ppm)	0.4	0.2
Fe (ppm)	5	2
Mg (ppm)	78	78
Mn (ppm)	3.1	3.1
P (ppm available)	38	47
K (ppm)	83	93
Na (ppm)	7	10
Zn (ppm)	8	.9
Sample Size	2	4

Given the small physical and chemical differences between soils (Table 3), the often significant differences in *Sorghum* tissue chemistry when grown on those soils (Table 4) were unexpected. Nitrogen and Zn were taken up in significantly greater amounts on the cyanobacterial-*Collema*-enriched soil, producing over 3.5 times more top growth than soils with no cryptobiotic growth (Fig. 3). The elements Ca, P, Mn, and Na were present in significantly greater concentrations in tissue of plants grown on the cryptobiotic-free soil. These data suggest that (1) N or Zn (probably the former) is limiting to plant growth in the test soil and (2) there is vigorous competition between the cyanobacteria and *Sorghum* for Ca, P, Mn, and Na.

It also seems clear that nutrient uptake by *Sorghum* was strongly affected by temperature in the root zone (Table 4). Nitrogen, Ca, Mg, Cu, and Zn were taken up in significantly larger amounts from the cyanobacterial-*Collema* soil at the higher temperature. Increased temperature seemed to intensify competition between the cyanobacteria and *Sorghum* for P, Fe, and Mn.

Preliminary [illegible] cyanobacteria [illegible] crust-free soils on infection of roots by rhizosymbionts show that 6 of 10 species evidenced infection by root symbionts (Table 5). Of those species whose roots showed some infection, 4 of 6 were annuals, and all infected annuals were colonized by vesicular arbuscular mycorrhizae (VAM). The degree of infection was always greater for plants grown in cyanobacterial-*Collema* crusted soil. Seedlings of the shrub *Coleogyne ramosissima* supported heavier VAM infection than associated annuals, and the relative amount of root colonized by the root symbiont was over three times greater when seedlings emerged from crusted soils. Roots of the perennial grass *Stipa hymenoides* always developed rhizosheaths on both types of surface, but the degree of sheath development was greatest on crusted surfaces (Table 5). The overall effect of crusted soils on root infection by symbionts was positive and statistically significant (Table 5).

DISCUSSION

The results presented provide strong support for the hypothesis that cryptobiotic soil surface covers (at least those rich in cyanobacteria) have significant effects on uptake of bioessential elements by associated seed plants. In this study we have considered only species (or developmental stages) with a major portion of their root system distributed in the surface 5 cm of soil. The cryptobiotic surfaces appear to consistently enhance uptake of some elements (e.g., N, K, Ca, Mg, and Zn), and to at least occasionally reduce uptake of other essential elements such as P, Fe, Mn, and Na (Tables 2, 4). Those effects are apparently partially explained by enrichment of soils (increased "availability" of essential elements) by cyanobacterial-*Collema* crusts (Table 1, 3), by elevation of soil temperature during cool seasons when moisture is most likely to be readily available for plant growth, and by greater likelihood of root colonization by mycorrhizal fungi and other root symbionts at sites that are stable enough to support well-developed cryptobiotic crusts. Our preliminary results also suggest that cyanobacterial-*Collema* crusts may result in an enhanced availability of certain elements through accelerated decomposition or production of chelating compounds (i.e., Mn and P in Table 1; Cu, N, Mg, and Zn in Table 4). Taken together, the data in Tables 3 and 4 suggest that the enhanced uptake of N by

TABLE 4. Tissue chemistry of aboveground growth of *Sorghum halepense* grown in cyanobacterial-*Collema*–free sand or sand heavily covered (over 80%) by cyanobacteria and *Collema* in pots wetted from the bottom. Also shown is tissue chemistry of *Sorghum* grown in the same cyanobacterial-*Collema*–stabilized sand held in deep, narrow rectangular planters. Averages followed by the same lowercase letter do not differ significantly ($p < .05$).

Tissue content of	Soil and potting conditions		
	Cyanobacterial-free soil in pots	Cyanobacterial soil in pots	Cyanobacterial soil in narrow planters
	- - - - - - - -	Concentration (% dry wt.)	- - - - - - - -
N	0.67 a	0.78 b	1.41 c
P	0.15 a	0.12 b	0.09 c
K	2.29 a	2.41 a	2.27 a
Ca	0.57 a	0.44 b	0.64 a
Mg	0.15 a	0.14 a	0.26 b
	- - - - - - - -	Concentration (ppm dry wt.)	- - - - - - - -
Cu	4.8 a	5.5 a	8.8 b
Fe	86.3 a	51.8 a	27.6 b
Mn	64.4 a	53.0 b	47.1 c
Na	114.3 a	32.6 b	50.7 c
Zn	15.7 a	22.6 b	23.9 b
Sorghum yield/pot (g-top growth only)	1.3 a	4.8 b	—
No. of replications	10	10	10
Avg. rooting zone temp (C)	~16	~16	~21

plants grown on crusted soils must include a considerable amount of N fixed simultaneously by cyanobacteria in the culture or N released by microorganisms decomposing the tissue of cyanobacteria grown during the experiment. Original differences in soil N were too small to account for the large differences observed in plant uptake in the two cultures.

Other studies have shown results similar to those reported here. Marble (1990) demonstrated that scalping the surface 1.0 cm of cyanobacterial-*Collema* crust around rosettes of *Lepidium montanum* var. *montanum* Nutt. two months prior to flowering significantly reduced aboveground plant weight and tissue content of K, Na, and Cu at flowering time. Several other elements (Ca, Mg, Fe, Mn, and Zn) were also lower in tissue of plants around which the cryptobiotic crust had been removed, but those differences were not statistically significant ($p >$ .05). J. Belnap (unpublished) has analyzed plant tissue for the annual *Streptanthella longirostris* (Brassicaceae) and seedlings of *Coleogyne ramosissima* (Rosaceae) grown on well-developed cyanobacterial-*Collema* crusts and on comparable soils without such crusts. Her data show that average plant size of both species was significantly larger on crusted soils, and tissue of both species contained significantly more N, Ca, Mg, and Cu per unit dry weight when grown on cryptobiotic surfaces. Belnap also has unpublished leaf chemistry data for adult shrubs of *Coleogyne ramosissima* and the long-lived, woody-rooted herb *Lepidium montanum* var. *jonesii* (Rydb.) C. L. Hitchc. As one might have predicted, adult plants of these species showed no enhancement of essential mineral uptake while growing on cyanobacterial-rich crusts. The vast majority of their feeder roots lie well below those portions of the soil profile that are influenced by cryptobiotic crusts.

As seen in Table 4, *Sorghum* growth was severely limited on soils free of cyanobacterial-*Collema* inoculum (Fig. 3). Nitrogen seemed inadequate in such soils to support healthy growth of *Sorghum*. In fact, growth was so minimal

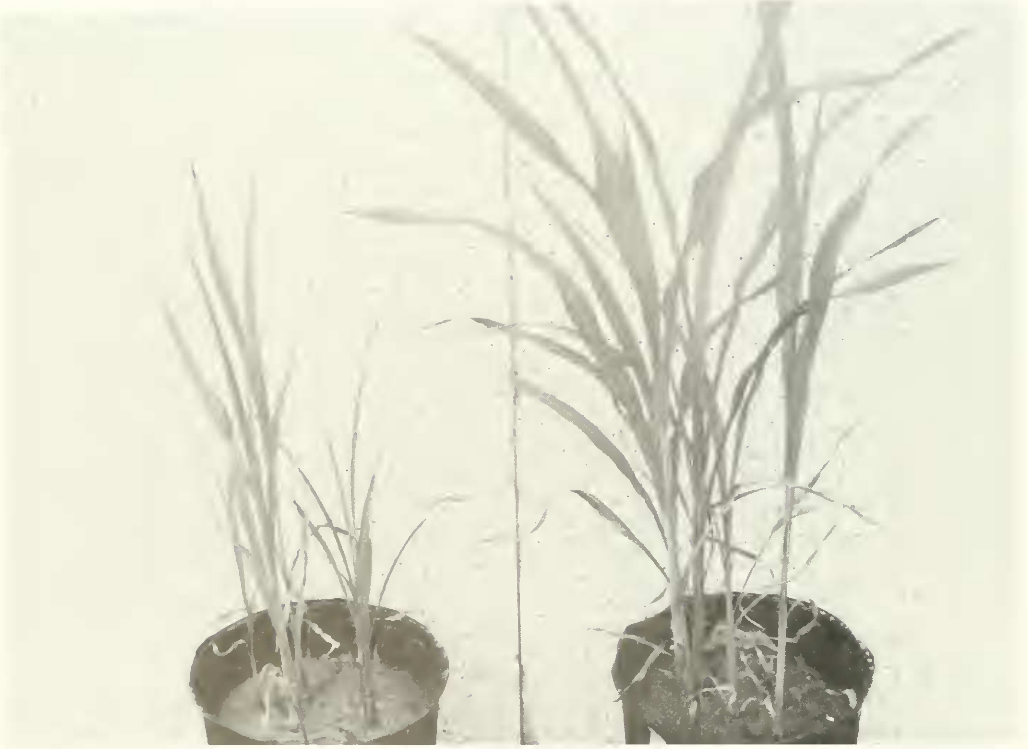

Fig. 3. *Sorghum halepense* plants after 60 days of growth on a soil mixture consisting of the surface 5 cm of a sand colonized by a heavy growth of cyanobacteria and *Collema tenax* (R) and the same depth horizon from a nearby site kept free of such growth by foot traffic (L). See Table 3 for characteristics of the two soils.

in those soils that the species would probably never have flowered and set seed on that substrate. When *Sorghum* was grown on a soil enriched by inclusion of the cyanobacterial-*Collema* inoculum, growth was much greater even though only N and Zn occurred in significantly greater concentrations in the tissue (i.e., all other essential elements occurred in higher concentration in plants grown on cryptobiota-free soil). These results suggest that even though cyanobacterial-rich crusts sometimes enhance uptake of several essential elements, plant growth (at least *Sorghum* growth) was limited by N (and perhaps Zn) only on the soil considered.

Evidence does exist that the cryptobiotic surface layers (especially those rich in cyanobacteria and/or cyanolichens) have a beneficial influence on seedling establishment under field conditions. Harper and Marble (1988) summarize the results of an experimental seeding of five species onto plots dominated by cyanobacteria and the lichen *Collema*. At time of seeding, [illegible] plots were randomly chosen for a treatment in which the surface 1.0 cm of cryptobiotic crust was scalped away. Each species was seeded on 10–22 randomly chosen plots through a template at 32 locations per 1.0-m^2 plot. After the first growing season four of the five species had more seedlings on plots where the cryptobiotic crust was left intact; in total there were slightly over three times as many seedlings on the average crusted plot as on the average scalped plot. After three years a larger percentage of the seedlings survived on crusted than on scalped plots for all five species tested.

In Nevada, Eckert et al. (1986) planted seeds of six species on three types of surfaces: (1) those covered by a sparse plant litter cover and beneath a shrub canopy, (2) polygonal patterned surfaces covered by a vigorous growth of cryptogamic cover, and (3) polygonal patterned surfaces with little cryptogamic cover and in interspaces between shrubs as was surface type 2. Five of the six species tested established as well on the type 2 surface as on other surface types or even better on type 2 surfaces; the other species established best on type 3 surfaces

TABLE 5. Percentage of the root length colonized by rhizosymbionts on cyanobacterial crusted or comparable soils without a biotic crust. Roots of five randomly chosen plants were examined per species and soil surface condition. The effect of cyanobacterial crusts (treatment) on amount of colonization of roots by rhizosymbionts is significantly positive (F-value for ANOVA = 7.94, $p < .01$, d.f. = 1). F-value for species effects was 8.26 ($p < .01$, d.f. = 5). *Plantago patagonica* was omitted from the latter analysis.

Species °	Associate microbe	No biotic crust	Cyanobacterial crust
		- - - - - Avg. percent of root length colonized	- - - -
Bromus tectorum	VA mycor.[1]	3	8
Coleogyne ramosissima[2]	VA mycor.	5	18
Festuca octoflora	VA mycor.		
Colorado Plateau		T	1
Washington County		2	4
Lupinus pusillus	*Rhizobium*	22	34
Plantago patagonica	VA mycor.	No sample	13
Stipa hymenoides	Rhizosheaths[3]	40 (all weak)	100 (60% strong)

° Roots of the following species were studied, but no mycorrhizae were observed: *Cryptantha pterocarya*, *Cryptantha crassisepala*, *Mentzelia albicaulis*, and *Streptanthella longirostris*. All of these species are annuals.

[1] Vesicular arbuscular mycorrhizae

[2] Only seedlings arising from rodent caches were examined for this species.

[3] Rhizosheaths are dense tangles of root hairs, cells of a *Bacillus polymyxa*-like bacterium capable of N-fixation, and adherent sand grains (Wullstein and Pratt 1981)

and did poorly on type 2 surfaces. Lesica and Shelly (1992) reported that cryptogamic soil surface cover appeared to increase survival of established plants of *Arabis fecunda* Rollins (Brassicaceae) in Montana.

The foregoing reports suggest that establishment and survival of seed plants native to arid lands may often be enhanced by cryptobiotic cover on soil surfaces. As Harper and Marble (1988) show, several scientists have successfully used inocula of cyanobacteria to increase establishment and growth of agricultural crops in various parts of the world. Accordingly, observations of positive interactions between cyanobacterial-rich crusts and seedling establishment and growth in natural arid land environments are not surprising.

Although the influence of cyanobacterial-rich soil crusts on essential mineral uptake by associated seed plants appeared to be strongly beneficial for N only, there is reason to believe that enhanced tissue content of N, Ca, Mg, Na, and P may be beneficial to associated herbivorous and granivorous animals. Robbins (1983) notes that increased dietary protein consistently hastens growth and onset of reproductive maturity in herbivorous animals. Cyanobacterial crusts consistently increased protein content of associated shallow-rooted seed plants and seedlings of deeper-rooted plants in this study (Tables 2, 4; Belnap personal communication). Aumann (1965), Aumann and Emlen (1965), Belovsky (1981), and Robbins (1983) suggest that sodium in plant tissues is often inadequate to maintain healthy herbivores. Robbins's (1983) review of dietary sodium requirements for animals suggested that diets with less than 500 ppm sodium will eventually result in poor growth or death of animals. We note that cyanobacterial crusts always enhanced plant tissue content of Na in this study (Tables 2, 4). In our study, however, even plants grown on crusts did not contain the recommended minimum content of Na. Thus, animals must resort to local "mineral licks" to obtain adequate Na. Such licks may be widely spaced on sandy uplands such as those sampled for this report. Small mammals such as the granivorous heteromyid rodents common on deserts considered here may be especially dependent on Na in plant tissue, since they defend small territories that would rarely include a lick where supplementary minerals could be acquired. In such cases, increased tissue content of Na in plants growing on cyanobacterial-rich surface crusts may be of critical importance to associated heteromyid rodents.

Robbins (1983) considered that "calcium deficiencies are probably the major mineral problem encountered in captive wildlife." He noted that Ca and P are major constituents of the vertebrate skeletal system. In mature animals, 90% of Ca and 80% of P occur in bone, which has a Ca:P ratio of about 2:1. Since these elements are so intricately associated in bone, they are often discussed together. Birds use Ca not only in bone but also in eggshells, which are 98% $CaCO_3$ and less than 1% P. Osteoporosis is related to deficiencies in Ca and/or P in the diet or to major imbalances in their presence in the food base. Osteoporosis has been reported for free-ranging carnivores in Alaska, for reindeer on lichen-dominated ranges, and for the desert tortoise, a herbivore, from the warm deserts of southwestern Utah (Jarchow 1987, Robbins 1983). Carnivores may be especially prone to osteoporosis since flesh contains little calcium. Osteoporosis in the desert tortoise is surprising; Jarchow (1987) considered the disease to be a principal cause of death for the tortoise in Utah. He found the onset of osteoporosis to be premature and pathogenic in the animals examined. No disease could be shown to be associated with osteoporosis; thus Jarchow (1987) concluded that the condition was caused by dietary deficiencies. Since the principal food plants taken by the tortoise in southwestern Utah (Hansen et al. 1976) do not appear to be deficient in Ca (Jarchow 1984), the limiting element is probably P. Jarchow's (1984) and our own data (Tables 2, 4) both show less P in plant tissue than is considered necessary by Robbins (1983).

Since growth on cryptobiotic crusts has been observed to increase plant tissue content of P in *Festuca octoflora* (Table 2), *Coleogyne ramosissima* seedlings, *Lepidium montanum* var. *jonesii* (Belnap personal communication), and *L. montanum* var. *montanum* (Marble 1990), and to have no effect on tissue P content in *Streptanthella longirostris* (Belnap personal communication), it seems possible that cryptobiotic crusts could affect dietary intake of P by the desert tortoise. Since our data show that P is also occasionally lower in plants growing on cyanobacterial crusts (e.g., *Mentzelia* in Table 2 and *Sorghum* in Table 4), more research is needed to determine whether widespread coverage of cryptobiotic crusts would increase or decrease available P in the diet of the tortoise. Inasmuch as this species is formally listed as endangered and does appear to be susceptible to osteoporosis in nature, it is important that the influence of cryptobiotic crusts on nutritive quality of tortoise food plants be better understood. Cyanobacterial-lichen crusts are known to occur in southwestern Utah deserts, formerly the [illegible] for the tortoise ([illegible] and Masslich 1985), and their importance in those environments is also known to have been severely depleted by uses imposed by European man (Anderson et al. 1982, Callison et al. 1985). Restored vigor of those crusts may improve dietary quality for desert tortoises.

Although Robbins (1983) concluded that Mg rarely poses a dietary problem for herbivores, Grunes et al. (1970) and Fairbourn and Batchelder (1980) suggest that less than 0.25% Mg in the forage base puts ruminant animals at risk for grass tetany, a nutritional disease resulting in vasodilation, hyperirritability, and muscle damage, and possibly culminating in paralysis and death. Magnesium is an essential element for proper bone and tooth formation and is an important enzyme activator for all animals. Absorption of Mg by the digestive organs is apparently inhibited by high levels of N and K in the forage; thus, grass tetany is most often observed when animals are feeding on lush spring growth of grasses. We note that Hansen et al. (1976) found that annual grasses make up 68% of the desert tortoise's diet in southwestern Utah. Our data show that cryptobiotic crusts consistently enhanced Mg content of tissue of associated plants (Tables 2, 4). We suggest that the influence of cryptobiotic crusts on Mg in plants eaten by the desert tortoise merits further attention.

ACKNOWLEDGMENTS

This work was partially supported by a subcontract from the Shrub Sciences Laboratory, Intermountain Research Station, U.S. Forest Service at Provo, Utah. The contract was funded by the U.S. Army Corps of Engineers, Construction Engineering Laboratory, Champaign, Illinois. We thank J. Belnap for permitting us to review unpublished data from her files. The PCA analyses presented in Figure 2 were performed by Jeffrey Johansen, John Carroll University, University Heights, Ohio.

LITERATURE CITED

Allen, M. F. 1991. The ecology of mycorrhizae. Cambridge University Press, Cambridge, United Kingdom. 184 pp.

Ambler, J. R., and J. L. Young. 1977. Techniques for determining root length infected by vesicular-arbuscular mycorrhizae. Soil Science Society of America Proceedings 41: 551–556.

Anderson, D. C., K. T. Harper, and R. C. Holmgren. 1982. Factors influencing development of cryptogamic crusts in Utah deserts. Journal of Range Management 35: 180–185.

Aumann, G. D. 1965. Microtine abundance and soil sodium levels. Journal of Mammalogy 46: 594–604.

Aumann, G. D., and J. T. Emlen. 1965. Relation of population density to sodium availability and sodium selection by microtine rodents. Nature 208: 198–199.

Belovsky, G. E. 1981. A possible population response of moose to sodium availability. Journal of Mammalogy 62: 631–633.

Belnap, J., and K. T. Harper. 1993. The influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. In review.

Bethlenfalvay, G. J., R. A. Evans, and A. L. Lesperance. 1985. Mycorrhizal colonization of crested wheatgrass as influenced by grazing. Agronomy Journal 77: 233–236.

Black, C. A. 1968. Soil-plant relationship. 2nd ed. John Wiley and Sons, Inc., New York. 790 pp.

Black, C. A., D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clark, eds. 1965. Methods of soil analysis, part 1: Physical and mineralogical properties, including statistics of measurement and sampling. American Society of Agronomy, Inc., Madison, Wisconsin. 770 pp.

Booth, W. E. 1941. Algae as pioneers in plant succession and their importance in erosion control. Ecology 22: 38–46.

Brotherson, J. D., and W. J. Masslich. 1985. Vegetation patterns in relation to slope position in the Castle Cliff area of southern Utah. Great Basin Naturalist 45: 535–541.

Callison, J., J. D. Brotherson, and J. E. Bowns. 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwestern Utah. Journal of Range Management 38: 535–538.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Eckert, R. E., Jr., F. F. Peterson, M. S. Meurisse, and J. L. Stephens. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. Journal of Range Management 39: 414–420.

Egan, R. S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. Bryologist 90: 77–173.

Fairbourn, M. L., and A. R. Batchelder. 1980. Factors influencing magnesium in high plains forage. Journal of Range Management 33: 435–438.

Fletcher, J. E., and W. P. Martin. 1948. Some effects of algae and molds in the rain crust of desert soils. Ecology 29: 95–100.

Friedmann, E. I., and M. Galun. 1974. Desert algae, lichens, and fungi. Pages 165–212 *in* G. W. Brown, Jr., ed., Desert biology. Academic Press, New York.

Fritsch, F. E. 1922. The terrestrial algae. Journal of Ecology 10: 220–236.

Fuller, W. H., R. E. Cameron, and N. Raica. 1960. Fixation of nitrogen in desert soils by algae. Working papers of seventh congress of International Society of Soil Science for 19 August. Madison, Wisconsin.

Giovannetti, M., and B. Mosse. 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. New Phytologist 84: 489–500.

Glass, A. D. M. 1989. Plant nutrition: an introduction to current concepts. Jones and Bartlett Publishers, Boston, Massachusetts. 234 pp.

Grunes, D. L., P. R. Stout, and J. R. Brownell. 1970. Grass tetany of ruminants. Advances in Agronomy 22: 331–374.

Hansen, R. M., M. K. Johnson, and T. R. VanDevender. 1976. Foods of the desert tortoise (*Gopherus agassizi*) in Arizona and Utah. Herpetologia 32: 247–251.

Harper, K. T., and J. R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. Pages 135–169 *in* P. T. Tueller, ed., Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Dordrecht.

Jarchow, J. 1984. Veterinary management of the desert tortoise, *Gopherus agassizi*, at the Arizona-Sonoran Desert Museum: a rational approach to diet. Pages 83–94 *in* M. W. Trotter, ed., Proceedings, 1984 symposium of the Desert Tortoise Council, Long Beach, California.

______. 1987. Report on investigation of desert tortoise mortality on the Beaver Dam Slope, Arizona and Utah. Unpublished report to Arizona Strip and Cedar City Districts, Bureau of Land Management, St. George, Utah.

Kleiner, E. F., and K. T. Harper. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecology 53: 299–309.

______. 1977a. Soil properties in relation to cryptogamic ground cover in Canyonlands National Park. Journal of Range Management 30: 202–205.

______. 1977b. Occurrence of four major perennial grasses in relation to edaphic factors in a pristine community. Journal of Range Management 30: 286–289.

Koide, R. T., and H. A. Mooney. 1987. Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. New Phytologist 107: 173–182.

Koske, R. E., and J. N. Gemma. 1989. A modified procedure for staining roots to detect VA mycorrhizae. Mycological Research 92: 486–488.

Lange, W. 1974. Chelating agents and blue-green algae. Canadian Journal of Microbiology 20: 1311–1321.

______. 1976. Speculations on a possible essential function of the gelatinous sheath of blue-green algae. Canadian Journal of Microbiology 22: 1181–1185.

Lefevre, M. 1964. Extracellular products of algae. Pages 337–367 *in* D. F. Jackson, ed., Algae and man. Plenum Press, New York.

Lesica, P., and J. S. Shelly. 1992. Effects of cryptogamic soil crust on the population dynamics of *Arabis fecunda* (Brassicaceae). American Midland Naturalist 128: 53–60.

MacGregor, A. N., and D. E. Johnson. 1971. Capacity of desert algal crusts to fix atmospheric nitrogen. Soil Science Society of America Proceedings 35: 843–844.

MacKenzie, H. J., and H. W. Pearson. 1979. Preliminary studies on the potential use of algae in the stabilization of sand wastes and wind blow situations. British Phycology Journal 14: 126.

Marble, J. R. 1990. Rangeland microphytic crust management: distribution, grazing impacts, and mineral nutrient relations. Unpublished doctoral dissertation, Brigham Young University, Provo, Utah. 76 pp.

Mayland, H. F., and T. H. MacIntosh. 1966. Availability of biologically fixed atmospheric nitrogen-15 to higher plants. Nature 109: 421–422.

Mayland, H. F., T. H. MacIntosh, and W. H. Fuller. 1966. Fixation of isotopic nitrogen in a semi-arid soil [illegible] Soil Science Society of America Proceedings [illegible]

[illegible] 198[illegible]. [illegible] hyphal [illegible] microfungal populations: a study from gypsiferous soils of a Utah desert. Unpublished master's thesis, Brigham Young University, Provo, Utah. 21 pp.

PAGE, A. L., R. H. MILLER, AND D. R. KEENEY, EDS. 1982. Methods of soil analysis, part 2. Chemical and microbiological properties. 2nd ed. American Society of Agronomy, Inc., Madison, Wisconsin. 1159 pp.

PERRY, D. A., M. P. AMARANTHUS, J. G. BORCHERS, S. L. BORCHERS, AND R. E. BRAINERD. 1989. Bootstrapping in ecosystems. Bioscience 39: 230–237.

PIELOU, E. C. 1984. The interpretation of ecological data. John Wiley and Sons, New York. 263 pp.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, Inc., New York. 343 pp.

ROMNEY, E. M., A. WALLACE, AND R. B. HUNTER. 1978. Plant response to nitrogen fertilization in the northern Mohave Desert and its relationship to water manipulations. Pages 232–243 *in* N. E. West and J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

RYCHERT, R., J. SKUJINS, D. SORENSEN, AND D. PORCELLA. 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. Pages 20–30 *in* N. E. West and J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

SCHLESINGER, W. H. 1991. Biogeochemistry: an analysis of global change. Academic Press, New York. 443 pp.

SHIELDS, L. M., AND L. W. DURRELL. 1964. Algae in relation to soil fertility. Botanical Review 30: 92–128.

SKUJINS, J., AND B. KLUBEK. 1978. Nitrogen fixation and denitrification in arid soil cryptogamic crust microenvironments. Pages 543–552 *in* W. Krumbein, ed., Environmental biogeochemistry and geomicrobiology. Vol. 2. Ann Arbor Science, Ann Arbor, Michigan.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames. 593 pp.

STEWART, W. D. P. 1967. Transfer of biologically fixed nitrogen in a sand dune slack region. Nature 214: 603–604.

STEYN, P. L., AND C. C. DELWICHE. 1970. Nitrogen fixation by nonsymbiotic microorganisms in some California soils. Environmental Science and Technology 4: 1122–1128.

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Naturalist Memoir No. 9: 1–894.

WEST, N. E. 1978. Physical inputs of nitrogen to desert ecosystems. Pages 165–170 *in* N. E. West and J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

______. 1981. Nutrient cycling in desert ecosystems. Pages 301–324 *in* D. W. Goodall, R. A. Perry, and K. M. W. Howes, eds., Aridland ecosystems: structure, functioning and management. Cambridge University Press, Cambridge, United Kingdom.

______. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Advances in Ecological Research 20: 179–223.

WEST, N. E., AND J. SKUJINS. 1977. The nitrogen cycle in North American cold-winter semidesert ecosystems. Oecologia Plantarum 12: 45–53.

______. 1978. Summary, conclusions, and suggestions for further research. Pages 244–253 *in* N. E. West and J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

WULLSTEIN, L. H., M. L. BRUENING, AND W. B. BOLEN. 1979. Nitrogen fixation associated with sand grain sheaths (rhizosheaths) of certain xeric grasses. Physiologia Plantarum 46: 1–4.

WULLSTEIN, L. H., AND S. A. PRATT. 1981. Scanning electron microscopy of rhizosheaths of *Oryzopsis hymenoides*. American Journal of Botany 68: 408–419.